BIOMECHANICS OF WATER-PUMPING BY *CHAETOPTERUS VARIOPEDATUS* RENIER. SKELETOMUSCULATURE AND KINEMATICS

STEPHEN C. BROWN

Department of Biological Sciences, State University of New York, Albany, New York 12222

The tube-dwelling polychaete, *Chaetopterus variopedatus,* has long been recognized as being the most structurally specialized of all annelids. Although reasonably detailed and accurate accounts of the basic anatomy of *Chaetopterus* appeared near the turn of the century (Joyeux-Laffuie, 1890; Enders, 1909), the functional correlates of certain of the structural peculiarities have not been examined in detail. One of the most obvious gaps in our knowledge concerns the mechanism of water-pumping. *Chaetopterus,* like other aquatic animals which live totally confined within tube-houses or burrow systems, must actively irrigate its dwelling to provide an oxygen supply adequate to meet its respiratory demands. In addition, it has been shown that the filter-feeding mechanism of *Chaetopterus* is completely dependent upon the water-pumping activities of the animal (MacGinitie, 1939). It was early recognized that the three disk-shaped segments (numbers 14, 15, and 16) are the agents responsible for water propulsion, but the skeletomusculature of these particular segments has never been described in detail. Although a number of workers have considered different aspects of water propulsion by *Chaetopterus* (Berrill, 1927, 1928; Wells and Dales, 1961; Barnes, 1964, 1965), none has directly examined the mechanism involved. However, there appears to be general agreement that the behavior of the pump segments does not involve a simple peristaltic or undulatory motion—the two most common methods used by annelids to propel water through tubes. The present investigation was undertaken, therefore, to examine in detail the mechanism of water propulsion by *Chaetopterus.* This paper presents a description of the skeletomusculature and an analysis of the kinematics of the pump segments.

MATERIALS AND METHODS

Source and maintenance of animals

Specimens of *Chaetopterus* were obtained from Pacific Bio-marine Supply Co., Venice, California. In the laboratory, the animals, within their natural tubes, were maintained at 16° C in aerated recirculating aquaria containing 50 gallons of artificial seawater ("Instant Ocean", Aquarium Systems, Inc., Cleveland, Ohio). The worms were fed *ad libitum* daily with "Fryfare" extra-fine fish food.

Observational techniques

Since the animals could not be viewed directly in their natural tubes (due to the opacity of the tube wall), the worms were placed in glass tubes of equivalent

FIGURE 1. *Chaetopterus* in a glass observation tube which has been lined with the natural tube material. Terminal constrictions indicated by arrows; roman numerals correspond to the three pumping segments.

diameter prior to observation. Within 2 days after transfer, they had lined the glass tubes with a thin, transparent film of their natural tube material and had constructed the characteristic terminal constrictions at the ends of the tubes (Fig. 1). The environment immediately surrounding the worms, therefore, was nearly identical to that of the natural situation. Two lines of evidence, moreover, suggest that the pumping behavior of *Chaetopterus* in the observation tubes was well within the normal limits of behavior patterns of the worms in nature. First, pumping activity, as measured by the "surge-chamber" method of Wells and Dales (1951), or by pressure transducers, yielded identical data for worms in natural tubes and worms in lined glass tubes. Secondly, individual specimens of *Chaetopterus* have been maintained in a healthy condition in such lined glass tubes for over six months in our aquaria, indicating that the feeding mechanism (which is completely dependent upon pumping activity) is unimpaired. It would appear unlikely, therefore, that the pumping behavior of the worms, at least at the biomechanical level, was adversely affected by the substitution of glass tubes for the natural ones.

Prior to filming, a glass tube containing an active, acclimatized worm was placed in the viewing chamber shown in Figures 2 and 3. This chamber was made of $\frac{3}{16}$ inch plexiglas on the sides and bottom, with $\frac{1}{16}$ inch sheet glass for front and rear walls. Two front-surfaced mirrors inclined at 45° angles, together with appropriate illumination and masking, allowed simultaneous filming of top and side views of an actively pumping worm. Interconnected two-liter reservoirs at each end of the glass tube permitted the worm to pump water in either direction without development of an asymmetric pressure head. These reservoirs likewise served as sites where oxygenation and food addition could be accomplished without disturbing the animal. All observations were made at water temperatures of 16° C. Local heating effects during filming were minimized by interposing a 4 inch thick water-filled heat absorber between the light source and the viewing chamber. In addition, the viewing chamber itself was water-filled, thereby improving the optics of the system as well as acting as a second heat-absorber. Filming was done with a motor-driven Bolex 16 mm movie camera (at 16 and 24 f.p.s.) or with a motor-driven Nikon 35 mm single-lens reflex (at 4 f.p.s.). Kodak Plus-X negative film was used in either case. Frame-by-frame analysis of the 16 mm film was carried out with the aid of a L.W. Photo-optical Data Analyzer.

Anatomical methods

For detailed examination of the musculature, specimens were fixed by injection/ immersion in cacodylate-buffered 6.5% glutaraldehyde (pH 7.2) and subsequently
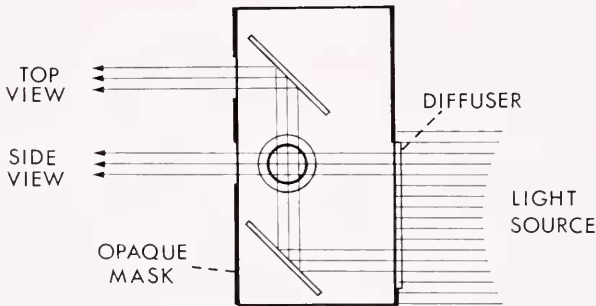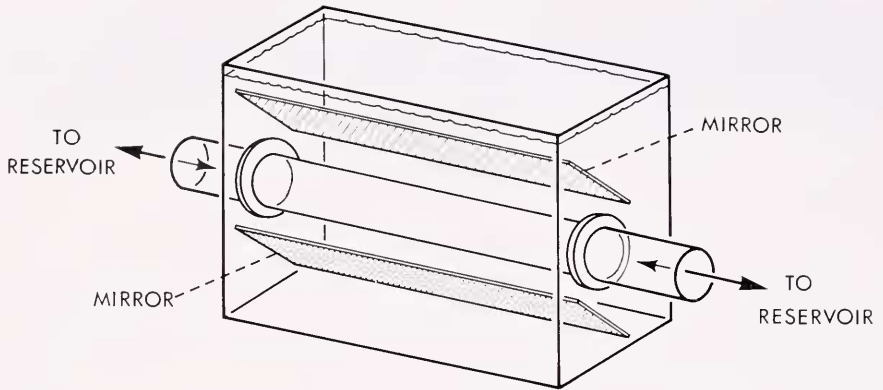
FIGURE 2.   Observation chamber; see text for details of construction.
FIGURE 3.   End view of observation chamber showing optics of system.

differentiated in 1% osmium tetroxide.   Dissections were performed with the aid of a Bausch and Lomb stereomicroscope.

RESULTS

Skeletomusculature

As in all annelids, the functional skeleton of *Chaetopterus* is hydrostatic. Coelomic fluid occupies an estimated 85% of the volume within each piston segment, with intestine, nephridia, and gametes making up the balance.   There is good anatomical evidence (Joyeux-Laffuie, 1890; Enders, 1909; Meissner, 1935) that the coelomic fluid contained within each piston segment is completely isolated, and my own experience with dye and fixative injection, or fluid removal, is consistent with this view.   Likewise, there were no indications during the present study that the volumes of the piston segments varied during pumping activity.

The general body wall of *Chaetopterus* is known to be unusually thin and elastic for a polychaete of its size (Storch and Welsch, 1970; Brown, Bdzil, and Frisch, 1972), and this is especially true for the integument of the pumping segments. Previous studies indicate that, with regard to external morphology and developmental homology (Joyeux-Laffuie, 1890; Enders, 1909), coelomic cavity and gonoduct structure (Meissner, 1935), and nervous system structural organization (Berrill, 1927), the three pump segments can be considered equivalent. The present investigator likewise found no differences in the muscular organization, and, accordingly, the description that follows applies equally well to each of the three pump segments.

Figure 4 shows the musculature visible within the right half of a piston segment, following removal of the intestine and nephridium. The so-called neuropodial "sucker" forms a base across which lies the large right ventral longitudinal muscle. Along the inner face of the posterior wall the thin transverse muscle fibers run in parallel courses. On the anterior wall the right promotor muscle ascends from its origin on the ventral longitudinal muscle and fans out dorsally, ultimately to terminate at multiple insertion points. Looking deeply into the contiguous parapodial cavity, one can see three distinct sets of muscles running across the cavity between anterior and posterior walls. These include: numerous fine distal parapodial fibers, which occupy the greatest area of the parapodial margin; more robust proximal parapodial muscle bands, which incompletely divide the parapodial cavity from the main chamber; and oblique parapodial muscle bands, which originate together anteriorly at the ventral longitudinal muscle, radiate in a dorsoventral plane, and ultimately terminate at numerous insertion points along the posterior wall. The relationship of distal and proximal parapodial muscles can be further seen in Figure 5, which shows a frontal section taken approximately midway along the dorsoventral axis. The anterior wall, as viewed from the interior, appears as shown in Figure 6. The large promotor muscles originate ventrally and terminate centrally at the midline, and laterally at, or near, the points of insertion of the proximal parapodial muscle bands. In the central region are also found numerous closely-spaced anterior radial (I) fibers. At the margin of the front wall are located peripheral anterior radial (II) fibers and submarginal fibers running parallel to the edge (anterior circular fibers). The musculature of the posterior wall of a piston segment is shown in Figure 7, as seen from the outside. The central region is dominated by a complex web of decussating fibers arising from left and right remotor bundles. Remarkably, these remotor bundles originate within the musculature of the ventral neuropodial "sucker" of the *adjacent* posterior segment, and thus are clearly *intersegmental* in nature. Circular and radial muscle fibers occupy the margin of the posterior wall, with their relative position being reversed from that found in the anterior wall. As previously shown (Fig. 4), the inner surface of the posterior wall contains a sheet of parallel transverse fibers.

Posture, orientation, and position during water-pumping

During most periods of active pumping, the worms are extended to approximately 1.5 times their fully-contracted length. The major contribution to this extended posture occurs in segment 13 (bearing the cupula), and to a lesser,
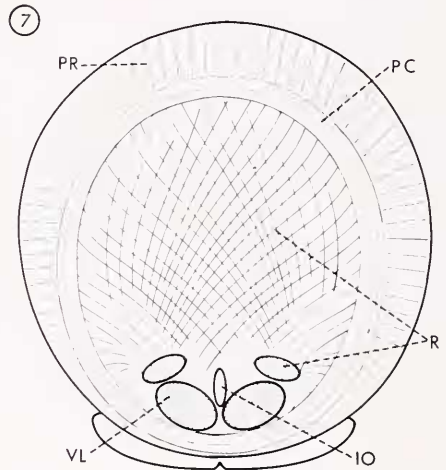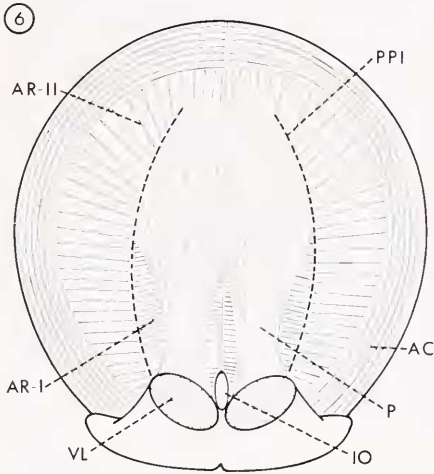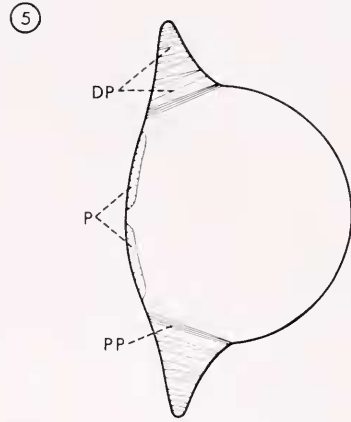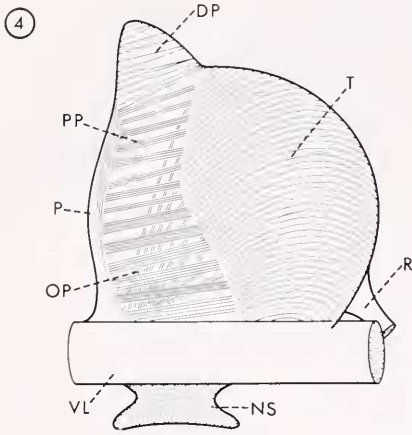
FIGURE 4. Musculature within right half of a pump segment: DP, distal parapodial; PP, proximal parapodial; OP, oblique parapodial; P, promotor; VL, ventral longitudinal; NS, neuropodial "sucker"; R, remotor; T, transverse.

FIGURE 5. Musculature of a pump segment as seen in frontal section; PP, proximal parapodial; P, promotor; DP, distal parapodial.

FIGURE 6. Musculature of the anterior wall of a pump segment: PPI, proximal parapodial insertions; AC, anterior circular; P, promotor; IO, intestinal opening; VL, ventral longitudinal; AR-I, AR-II, central and peripheral anterior radial.

FIGURE 7. Musculature of the posterior wall of a pump segment; PC, posterior circular; R, remotor; IO, intestinal opening; VL, ventral longitudinal; PR, posterior radial.

but significant, extent by the water-propelling segments (14–16). Full extension is achieved by slow, forward locomotion of the anterior part of the worm (segments 1–12), while the posterior part of the animal (segments 17 and beyond) remains stationary. Within the observation tubes, the preferred orientation was ventral

side down, the entire length of the animal. The most common postural variant was that in which the anterior segments (1–12) skewed in either direction about the longitudinal axis, segment 13 would be twisted, and segments 14 and beyond would remain unaffected. Occasionally a worm would take up an inverted orientation (clinging to the roof of the tube), with or without a skewness in posture. Since all of the observation tubes were at least 5–10 cm longer than the worms, the animals had ample opportunity to move linearly within their tubes. The worms showed a decided preference for positioning themselves towards the temporary incurrent end, but neither opening was consistently chosen for this functional role. Although neither skewness nor inverted orientation appeared to alter pumping activity to any significant degree, all of the measurements reported here were taken from animals in the extended, axially-aligned posture and in the ventral-side-down orientation.

General characteristics of pumping activity

Figure 8 shows film records of the sequence of activities which occurs during one complete pump cycle. The most obvious component of the cycle is the axial displacement of the dorsal and lateral portions of segments 14–16. Close observation of individual piston segments further reveals that well-defined radial movements occur at specific intervals during axial displacement. During the backward (power) stroke, the margin of each pump segment is extended to meet the inner face of the tube wall; during the forward (recovery) stroke, the segmental margin is retracted, leaving a clearance, dorsally and laterally, between worm and tube wall. There exists a high degree of both intrasegmental and intersegmental coordination and it appears that segments other than numbers 14, 15, and 16 remain virtually motionless during pumping activity.

Displacements and shape changes

Eleven worms were filmed during active water-propulsion and the simultaneous axial and radial displacements of the dorsal and lateral margins of the piston segments were determined. To compensate for absolute size differences and rates of pumping, the data were normalized and then subjected to direct graphical comparison. Composite results are shown in Figures 9 and 10. These curves should be taken as "modes", rather than true arithmetic "means" of all of the worms measured. The time and distance marks are likewise indicative of mode values for worms weighing 6–9 gms, in aerated seawater at 16° C. In the clear majority of cases, the axial displacements (Fig. 9) approximated a pure sine function. In any single worm there were no detectable performance differences among the three piston segments. The only variation between worms which appeared more than once in the records occurred during the recovery phase, when the segments failed to initiate recovery immediately upon reaching their most posterior position. However, since the velocity of the subsequent recovery movement was always increased, the relative duration of the total recovery stroke remained at 50% of the complete cycle. All power phase records were virtually identical. Calculated velocity and acceleration curves, together with representative absolute values, are also given.

FIGURE 8. Sequence of activities during one complete pump cycle in *Chaetopterus* (anterior of worm to left); left-hand column as seen from side, right-hand column as seen simultaneously from top. Time between exposures is approximately 0.25 sec.
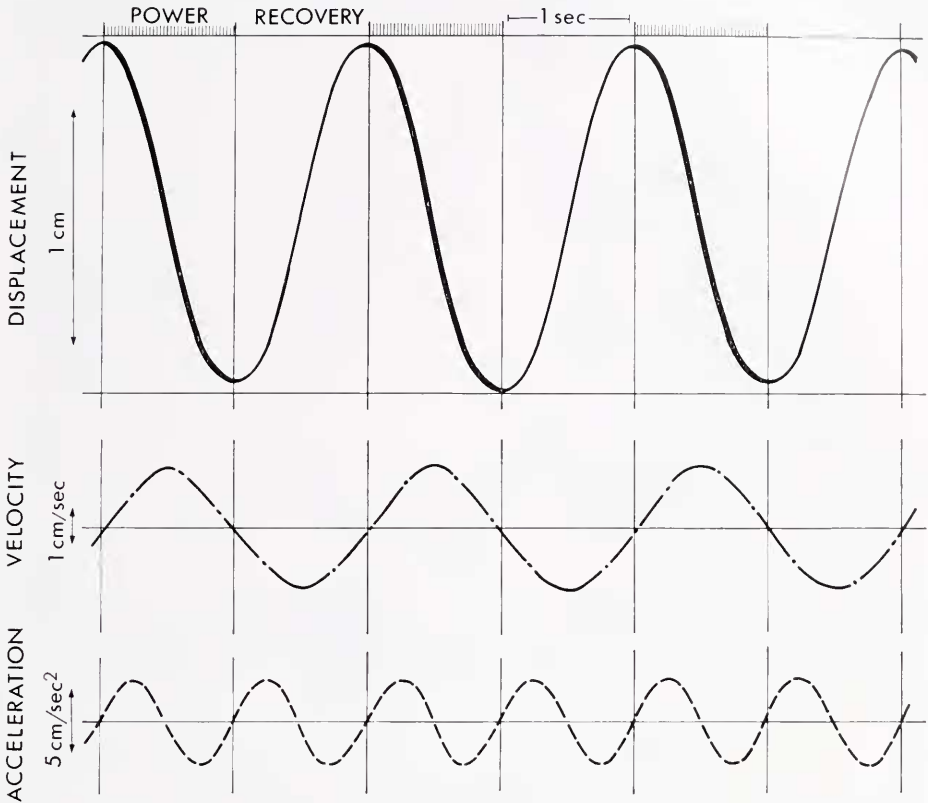
AXIAL PARAMETERS

FIGURE 9. Characteristic maximum axial displacements of the pump segment periphery during 3 consecutive pump cycles.

Modal characteristics for radial displacements are shown in Figure 10. The displacements here are clearly asymmetric, with the centrifugal movement limited by the inner margin of the tube wall. Although the total distances moved radially by the margins of the piston segments are less than $\frac{1}{4}$ of the distance moved axially, the radial movements are at least twice as rapid as the axial—as seen in the derived velocity/acceleration curves. Simultaneous plots of the axial and radial displacements yield the trajectories shown in Figure 11A. In order to evaluate the changes in shape which occur, selected frames from one complete pump cycle were projected and drawn in superimposed positions. Since no significant differences among the segments could be detected, the shape changes for only one segment are given in Figures 11B and 11C, for clarity. These latter figures clearly indicate the shape changes to be great, in spite of the fact that at all times during the pump cycle the piston segments remain nearly circular in cross-section. During the power phase, the mobile portion of a piston segment assumes a geometry which loosely approximates a biconvex disk. The inner wall of the
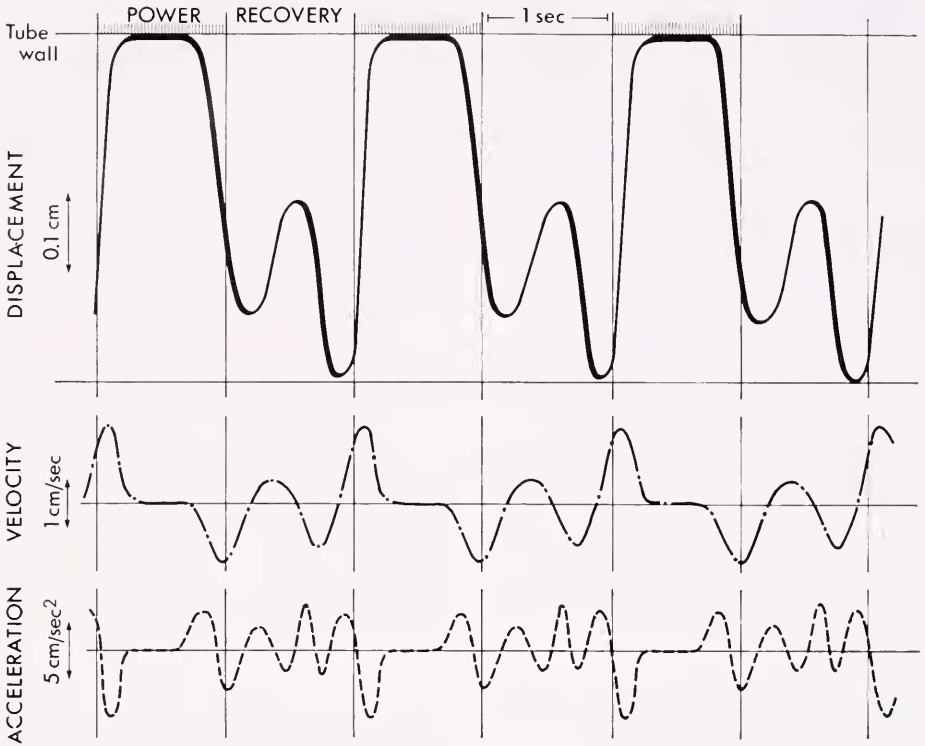
RADIAL   PARAMETERS

FIGURE 10.   Characteristic maximum radial displacements of the pump
segment periphery during 3 consecutive pump cycles.

tube sets a maximum limit on the amount of radial extension which can occur. During the initial part of the recovery stroke, the mobile portion of a piston segment rapidly assumes a nearly spherical shape.   The minimum diameter of this sphere is undoubtedly set by the volume of incompressible coelomic fluid contained within the segment.   Recovery is continued by a forward rocking/rolling motion, and the final transition from sphere to biconvex disk is rapidly accomplished at the climax of the recovery stroke.

Muscle action during the pump cycle

Although it was not feasible to record directly the sequence and duration of muscle contraction using standard myographic techniques, two features of the system made it possible to analyze the muscle activities with reasonable confidence of accuracy.   The first of these was the fact that although the total musculature of a piston segment is complex, the courses of individul sets of muscles are relatively simple and straightforward (the remotors being an obvious, but manageable, exception).   Secondly, the ability to record simultaneous top and side views of the
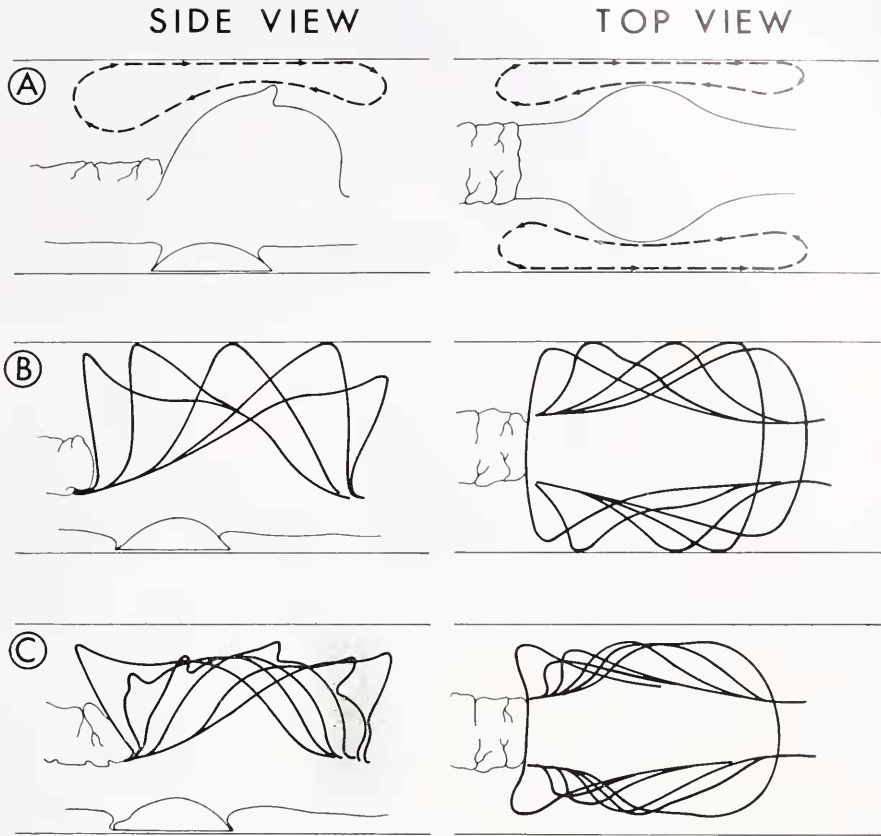
SIDE VIEW   TOP VIEW

FIGURE 11. (A) Trajectory (side and top view) of margin of pump segments during a complete pump cycle; (B) shape changes (side and top view) during the power stroke; (C) shape changes (side and top view) during the recovery stroke.

relatively slow shape changes (*ca.* 2 + seconds for a complete cycle) at relatively fast film speeds (24 f.p.s.) enabled the onset of even small absolute displacements (*e.g.,* in the radial direction) to be easily detected and measured. A diagram summarizing the deduced sequence, duration, and action of the various muscle groups during a single complete pump cycle is presented in Figure 12.

Starting at the 12:00 o'clock position on the diagram and proceeding clockwise, I will first consider the power stroke. Careful examination of the films and of the muscle anatomy indicates that the remotor muscles are entirely responsible for the rearward axial displacement. The functional origin of the remotors deep within the ventral "sucker" of the adjacent posterior segment provides a firmly fixed anchor point from which are generated the propulsive forces causing water movement. In addition, it is almost certain that the proximal parapodial muscles act to transmit the tensile force of the remotors *directly* to the anterior wall, although the proximal parapodial muscles do not perceptibly shorten during
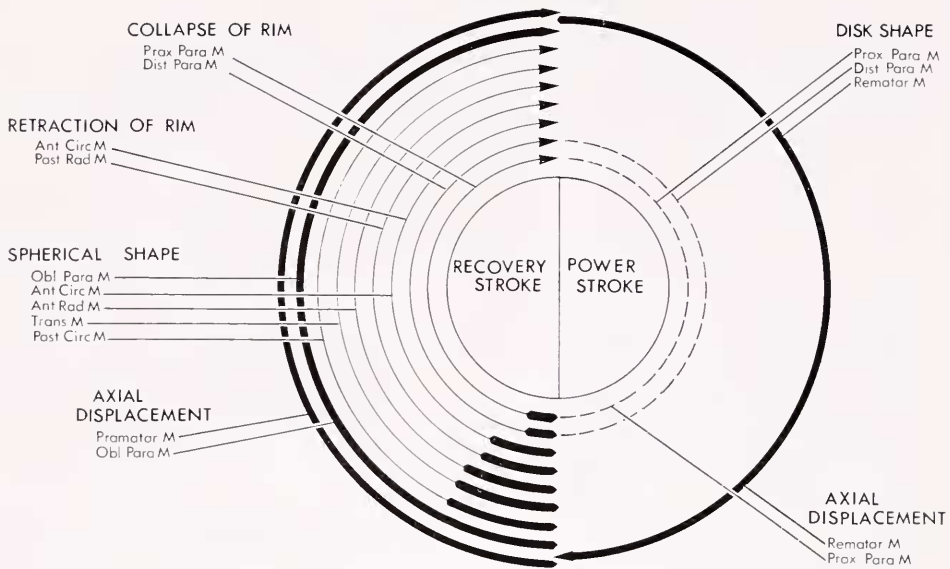
FIGURE 12. Proposed muscle action during pump cycle, see text for details; periods of muscle shortening indicated by broad lines; maintenance of maximal contraction, narrow lines; active or passive resistance to elongation, dashed lines; passive elongation, omitted.

this phase. It is not possible to state, however, whether the proximal parapodial muscles resist being stretched by actively maintaining tonus, or by simply being elongated to their maximum length. Contraction of the remotor muscles appears to be responsible for inflating the lateral (parapodial) margin and keeping it closely pressed against the inner margin of the tube during the power stroke (*i.e.*, in the extended "disk shape" configuration). [For any muscle set to cause such marginal inflation, its contraction must force coelomic fluid from the main cavity into the peripheral region *without* simultaneously reducing the circumference of the segment. Close inspection of Figure 11 reveals that during the latter phases of the recovery stroke, the posterior wall rapidly loses its hemispherical compound curvature and assumes a more flattened shape. The volume of the coelomic fluid "lost" from the main cavity consequent upon this configuration change is the likely source of fluid required to inflate the parapodial margin. The criss-crossing slips of the remotor muscles are the only fibers whose shortening can accomplish this shape change in the main cavity]. The final shape of the margin, however, cannot be determined solely by the remotor muscles. The integument in this region is likewise too thin and elastic to maintain such a shape by itself. Rather, the numerous distal parapodial fibers, traversing the parapodial cavity axially, must act as "guy wires" to limit the inflation of the marginal flange. Once again, whether they do this actively (by maintaining some contractural tonus) or passively (being simply at the limit of their stretched condition) is not known.

The first event whch occurs at the beginning of the recovery stroke is the axial collapse of the parapodial rim. This action is brought about by the contraction of the distal and proximal parapodial fibers, and results in the expulsion

of fluid formerly contained within the margin back into the main coelomic chamber. Starting at the same time, but requiring longer to complete, is a backward folding and radial retraction of the parapodial rim. This is brought about by shortening of the posterior radial and anterior circular fibers. Subsequently, at least five sets of muscles are involved in the basic shape change of the main chamber from disk to sphere configuration. These are the anterior and posterior circular, oblique parapodial, anterior radial, and transverse muscles. The forward axial displacement is brought about by contraction of the promotor muscles, with the probable aid of the oblique parapodial fibers. When forward recovery is complete, the transition from sphere to disk shape is caused by the initial phases of contraction of the remotor muscles.

Discussion

The mechanism by which *Chaetopterus* pumps water through its tube involves the coordinated activities of segments 14, 15, and 16. Each of these pumping segments acts functionally as a "piston" to drive a quantity of water axially within the tube. No differences could be detected in the skeletomusculature of the three piston segments, although the segments themselves are obviously not "identical" since they bear different positional relationships to one another. The majority of muscles run as thin sheets of parallel fibers immediately beneath the fragile, membranous integument. Even those muscles which originate as relatively massive "bundles" (*i.e.,* remotors and promotors), eventually flatten to thin sheets at their insertions. The proximal, oblique, and distal parapodial muscles remain as distinct fibers throughout their courses, and they are the only muscle groups to run from wall to wall across the coelomic cavity. As with any hydrostatic skeletal system, the musculature is responsible for two fundamental actions: (1) small-magnitude displacements, which help to determine segmental shape, and (2) large-magnitude displacements, which cause segmental motion (Chapman, 1950, 1957). The functional organization of the piston segments of *Chaetopterus* may be examined by assigning each muscle group to the following categories, as appropriate: (1) muscles causing axial displacements; (2) muscles causing radial displacements; (3) muscles operative during the power stroke; and (4) muscles operative during the recovery stroke (refer to Fig. 12). Comparison of categories 1 and 2 indicates that many more individual sets of muscles contribute to the radial displacements than contribute to the axial displacements. This, in part, may reflect the fact that radial expansion and retraction is basically a multiple-axis movement, while displacement back and forth along the tube is a uniaxial movement. Comparison of categories 3 and 4 reveals a similar unequal distribution, with far more individual muscle groups actively contracting during the recovery stroke than during the power stroke. However, it is a moot point whether the recovery-phase motions *per se* are more complex than those of the power phase. In this case mere numbers may be misleading since the single muscle set responsible for the power stroke is the largest and most complex of all those involved in pumping water.

The basic motion of the piston segments is reciprocative, and the primary displacements lie along the same axis as the water flow. In addition, there exists a set of secondary (radial) displacements perpendicular to the water flow. By virtue of their precise coordination, these two sets of displacements provide the

motions required for an operational positive-displacement pump—namely: (1) an initial centrifugal displacement, which culminates in the formation of a tightly-sealed "piston head" across the tube opening; (2) a power-stroke axial displacement, which moves the piston head and a quantity of water lengthwise down the tube; (3) a centripital displacement, which allows water to by-pass the piston head from the inlet end of the tube; and (4) a recovery-stroke axial displacement, which moves the piston head back to its initial starting position. It should be noted that the separation of piston-forming motions from water-propelling motions is paralleled, in each segment, by the (topographical) separation of the functional "piston ring" (which is limited to the outermost marginal rim) from the functional "piston head" (which encompasses virtually the entire posterior surface). The foregoing analysis applies equally well to the integrated 3-segment pump as to the individual components. The mechanical characteristics which are only applicable to the integrated pump mechanism will be discussed when the kinetics and hydrodynamics of the system are considered (S. C. Brown, in preparation).

The biomechanical characteristics outlined above for *Chaetopterus* stand in sharp contrast to the majority of annelid water-propulsion systems which are based upon peristalsis or undulation. In the latter cases, the basic motion of the functional piston surface approximates a simple transverse wave propagated axially, and the primary displacements (in the radial direction) are perpendicular to the flow of water. These simple radial displacements simultaneously accomplish both piston-forming and water-propelling functions. In addition, any surface which acts as a "piston ring" (or functional seal) also acts at some point in the pump cycle as a "piston head." These characteristics are seen even in those worms whose primary peristaltic irrigation movements are complicated by simultaneous axial displacements (*e.g.,* in *Sabella pavonina;* Mettam, 1969).

Perhaps the most distinguishing feature of members of the family Chaetopteridae is the diversity in their segmental structure. The extreme case is *Chaetopterus,* whose bodily organization strongly parallels the arthropod pattern of grouping adjacent segments into functional units (= "tagmatization"). It seems not unreasonable to suggest that the evolution of the unique pumping mechanism described above was made possible by the possession of a hydrostatic skeleton and, at the very least, facilitated by the tendency towards tagmatization. The exact origin of this pumping mechanism is not clear. Barnes (1964, 1965) appears to be the only investigator to have examined the other genera of chaetopterids with reference to their mechanisms of water-propulsion. Although those genera (*Spiochaetopterus, Telepsavus, Phyllochaetopterus*) considered to be least modified from their presumed spionid ancestors propel water entirely by ciliary means, the more advanced genera (*Ranzanides, Mesochaetopterus*) are reported to irrigate their tubes by a muscular "peristalsis" of many pumping segments "modified somewhat differently" from the three pump segments of *Chaetopterus* (Barnes, 1965, p. 231). In view of the fundamental differences between "peristalsis" and the reciprocating positive-displacement pump mechanism described herein, a closer study of the latter two genera is clearly merited.

Summary

1. The skeletomusculature of the water-pumping segments of *Chaetopterus variopedatus* was examined in detail and the behavior of the segments during active water-propulsion was analyzed using cinemaphotographic techniques.

2. The musculature of the pumping segments consists largely of thin sheets of radial, transverse, and circular fibers, located immediately beneath the thin integument. Exceptions to this are the numerous isolated fibers running axially across the coelomic cavity of the parapodial rim and the major remotor muscles which originate in the neuropodial "sucker" of the adjacent posterior segment.

3. The motion of the pump segments is basically reciprocative, with the axial displacement during power and recovery strokes approximating a sine function. Centrifugal radial displacements (during the power stroke) effectively seal the lumen of the tube; centripital radial displacements (during the recovery stroke) allow water from the inlet side of the tube to by-pass the pump segment.

4. Comparison of the muscle anatomy with the displacements and shape changes which take place during water-propulsion permitted analysis of the muscle actions during the pump cycle. It is concluded that: (a) both axial and radial displacements during the power stroke are caused by a single set of muscles (remotors); (b) maintenance of the extended-disk configuration is consequent upon coelomic fluid being forced into the parapodial rim, with the axial muscle fibers acting as guy-wires to resist overexpansion; (c) most of the sheet-like muscle groups contract during the recovery stroke, thereby causing the segment to assume a nearly spherical configuration; and (d) two sets of muscles (promotors, oblique parapodial) are responsible for the axial displacement during recovery.

5. The water-pumping mechanism of *Chaetopterus* is compared to those of the majority of worms, which are based on persistaltic or undulatory movements.

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